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Hypotheses on the Origin of Exploited Skipjack Tuna (Katsuwonus pelamis) in the Eastern and Central Pacific Ocean

By Brian J. Rothschild

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By

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ABSTRACT

A set of hypotheses has been formulated to account for the origin and movement of exploited groups of skipjack tuna (Katsuwonus pelamis) in the eastern and central Pacific Ocean. The hypotheses take into account the available evidence on larval distributions, gonad indices, size distributions, tag recoveries, catch predictions, and immunogenetic studies. The evidence suggests that most skipjack taken by the eastern Pacific skipjack fisheries originate in the central Pacific. It is likely that the equatorial region of the central Pacific contributes a major portion of the recruitment stock for the eastern Pacific. Large proportions of the Hawaiian catch also may originate in the Equatorial Zone. Skipjack catch predictions are discussed in the context of evidence which indicates that year-class-strength phenomena affect the Hawaiian landings. The need for more evidence on the origin and movements of harvested skipjack is emphasized.

INTRODUCTION

Skipjack tuna (Katsuwonus pelamis) are distributed throughout the tropical and subtropical Pacific Ocean. In recent years yields from Pacific skipjack fisheries have been of the order of 550 million pounds annually. There are now three major fisheries: the eastern Pacific fishery, in the coastal waters of North, Central, and South America from Baja California to Peru (161.4 million pounds in 1962); the Hawaiian fishery (9.4 million pounds in 1962); and the fishery off the Japanese archipelago (375 million pounds in 1962). Formerly there was a fishery in Micronesia, which produced 72.8 million pounds in 1937 (Shapiro, 1948: p. 59). Although this area has been virtually unfished for skipjack over the past 2 decades a fishery is now recommencing.

The apparent decline in eastern Pacific yellowfin tuna stocks being fished (e.g., Schaefer, 1961, 1962, 1963) and the increasing world demand for tunas (Chapman)[1/] suggest that fishing for skipjack may become greatly intensified, both in existing fishing areas and in areas not now fished. Management may eventually become necessary to ensure continued high yields of skipjack.

To place future investigations and possible management measures on a rational and economically sound basis, we need knowledge of the origins and relationships of the groups of skipjack that are being harvested or may be harvested in the future. A first step in organizing and enlarging this knowledge is the construction of a set of hypotheses incorporating available data into a testable, integrated picture of the population biology of the Pacific skipjack. The presentation of such hypotheses is the purpose of this paper. Since information from Japanese sources (e.g., Kawasaki, 1955) indicates that the skipjack caught off Japan originate from spawnings in the Ryuku-Izu-Bonin Islands area, far from the areas of direct concern to American fishermen, I will discuss only the origin and relationships of the skipjack of the eastern and central Pacific. I do not attempt to review all the literature on skipjack populations because adequate reviews have

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1/ Chapman, W. M. Recent trends in world tuna production and some problems arising therefrom. Paper presented to the Symposium on Scombroid Fishes. Marine Biological Association of India, Mandapam Camp, South India, 12-15 January 1962. (In press.)

recently been published by others (Waldron, 1963; Jones and Silas, 1963; Postel, 1963).

This paper collates the available evidence pertinent to the problem of the origin of the exploited groups of skipjack in the eastern and central Pacific Ocean and forwards hypotheses which, I believe, are consonant with such data. Its sections will cover, first, a brief statement of the hypotheses; secondly, the evidence upon which they are based, and finally a discussion of the hypotheses and the sometimes intuitive reasoning which led to their development.

The set of hypotheses has been generated from a consideration of a wide variety of data. Many of these data have been published by the Inter-American Tropical Tuna Commission (IATTC) and the Bureau of Commercial Fisheries. Other data have been obtained from the files of the Bureau's Biological Laboratory, Honolulu, and analyzed for this paper.

The hypotheses are based on a consideration of three conceptual zones from which the skipjack harvested in the eastern Pacific might originate (fig. 1). The hypotheses postulate that large proportions of skipjack which enter the eastern Pacific fishery originate in the Equatorial Zone. The predominant flow pattern for these fish is suggested in figure 2. At prerecruit size (< about 35 cm.) skipjack are continually dispersing from the equatorial central Pacific. A large component moves east toward the coast of the Americas; near the coast, one portion enters the Baja California fishery area while another moves into the Central and South American fishery areas.

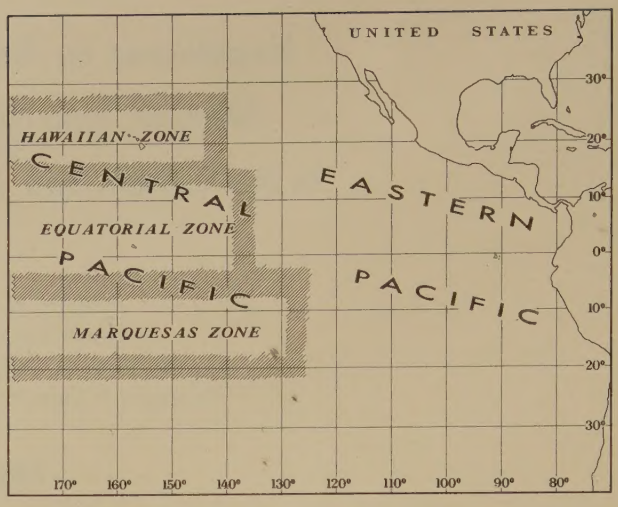

Figure 1.--Schematic representation of the conceptual areas that were evaluated in this paper.

The skipjack remain in the eastern Pacific for several months and may attain sizes of 55-65 cm. The attainment of this relatively large size (for the eastern Pacific) seems correlated with an offshore spawning movement. This offshore movement terminates in equatorial waters of the central Pacific where spawning occurs. An apparent north-south component of movement is superimposed on the generally easterly movement of "adolescent" prerecruits to the eastern Pacific fishery and the generally westward direction of the eastern Pacific spawning escapement. This north-south component may be a general dispersal affected by population density or it may be associated with the seasonal shift of the physical environment (e.g., temperature),

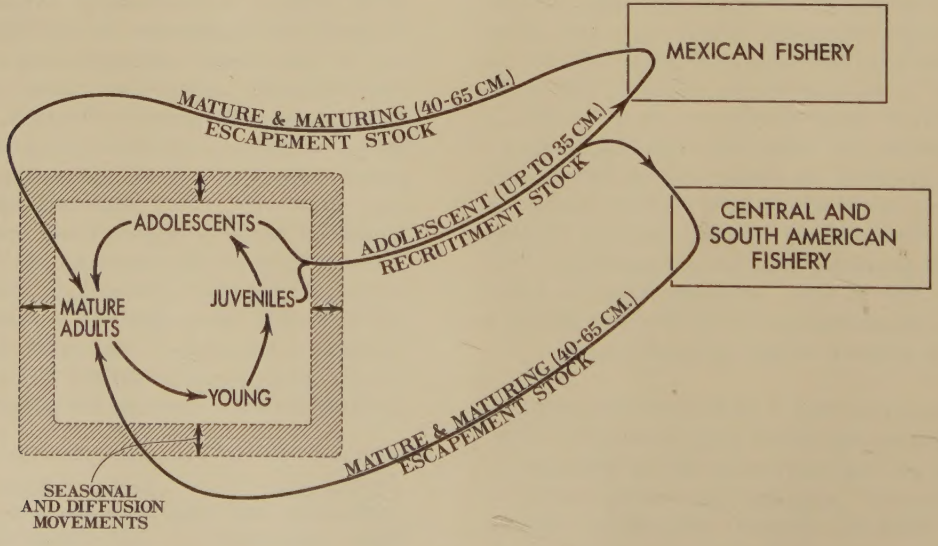

Figure 2.--Diagram showing the flow of skipjack between the central Pacific and the Mexican and South American fisheries of the eastern Pacific.

particularly in the more temperate latitudes. The maximum northward extension of the Equatorial Zone skipjack occurs during the northern summer, thus also accounting for a large proportion of the Hawaiian catch.

EVIDENCE

Data that seem pertinent to the problem of the origin of the exploited groups or subpopulations of skipjack have been selected from the literature. The data selected involve the distribution of spawning, length-frequency distribution of Hawaiian and eastern Pacific samples, a comparison of eastern and central Pacific length-frequency distributions, movements, prediction indices, and subpopulation structure. This section is, in effect, an appendix to the hypotheses section, but is presented here so that the reader can readily examine the background material before encountering a discussion of the various hypotheses.

Distribution of Spawning

Postlarval skipjack and advanced gonad indices have been used as evidence of skipjack spawning. Gonad indices are based on the relative size of the largest ova or the ratio of body weight to gonad weight. These indices are difficult to interpret, because running ripe skipjack are practically never taken; therefore, gonad or egg size indices only indicate maturity up to the level at which prespawning fish cease to be available to sampling. The time elapsing between cessation of availability and actual spawning is not known.

The distribution of the earliest identifiable larvae or postlarvae may be a better index of the temporal-spatial distribution of spawning than are gonad indices. This belief is based on the reasonable assumption that larvae and even postlarval skipjack have a much smaller degree of mobility than the adults and on a less defensible assumption that mortality in skipjack at these stages is approximately uniform with respect to time of year and location.

Evidence, based on the occurrence of larvae and juveniles, that skipjack spawn during a wide range of months over the enormity of the tropical Pacific should be viewed with caution. It is necessary to determine whether the capture of skipjack larvae or juveniles in incidental numbers in certain areas indicates that the spawning which occurs in those areas is great enough to make a measurable contribution to the exploited stocks.

Spatial distribution of larvae.--The distributions of skipjack larvae in the eastern and central Pacific are different, because larvae are taken in relatively high numbers in the central Pacific with 1-m. plankton nets, but almost none are caught with similar gear in the eastern Pacific. Klawe (1963) has undertaken the most complete study of the distribution of tuna larvae in the eastern Pacific Ocean. He examined a large number of plankton tows, representing samples taken by several types of gear at various depths. Only a few larval (about 0.02 larvae per tow) and juvenile skipjack were found. Klawe (p. 466) concluded that for skipjack there is "...very limited spawning in coastal and oceanic waters of the area of our study. Young forms [were] collected only on a few occasions, off Central America and as far north as the Gulf of Tehuantepec. Young [were] also collected off Ecuador." Since only a few skipjack larvae were taken in the eastern Pacific, no temporal patterns were ascertained from the data.

The relative absence of skipjack larvae in Klawe's data concurs with Matsumoto's (1958: p. 59) figure 31, which shows a drop in skipjack larvae per 1,000 $m.^3$ of water strained in the vicinity of long. 120° W. as compared with areas to the west.

With regard to latitudinal distribution of skipjack larvae, Matsumoto's (1958: p. 58) figure 30 shows apparently high densities of skipjack larvae in the equatorial region, with a reduction in numbers of larvae per 1,000 $m.^3$ of water strained as one proceeds northward from the Equator. Data in the files of the Bureau of Commercial Fisheries Biological Laboratory at Honolulu, the appendices of Matsumoto (1958) and Strasburg (1960), and Matsumoto's (1958) figure 33, for example, suggest that the Hawaiian Islands region, particularly in the summer, is also a locus of high densities of larval skipjack.

Temporal distribution of larvae.--The temporal distribution of tuna larvae in the central Pacific is known from Matsumoto (1958: p. 64), Nakamura and Matsumoto[2/], and miscellaneous data in the files of the Bureau's Biological Laboratory at Honolulu. It appears from these data that skipjack spawn the year-round in the equatorial region, with peak numbers of larvae per sample from May to September. In the Hawaiian Islands, spawning occurs primarily during the northern summer, whereas in the Marquesas,

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2/ Nakamura, Eugene L., and Walter M. Matsumoto. Manuscript. Distribution of larval tuna in Marquesan waters. Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

spawning occurs primarily during the northern winter.

Gonad indices.--Orange (1961) considered skipjack gonad indices for the several statistical areas defined by IATTC. In the northernmost of these areas, off Baja California, skipjack up to 73 cm. were examined; all of these fish had gonads in latent or resting states. Interestingly, the most nearly mature females in all areas of the eastern Pacific covered by that study were found just a short distance from Baja California, in the Revillagigedo Islands. Another area that yielded fish in a comparatively high state of maturity (although not as nearly "mature" as the fish from the Revillagigedo region) was the Cocos Island region. This region and the Revillagigedos are the only places in the eastern Pacific where relatively high proportions of maturing skipjack were found. None of the coastal areas, from Baja California to Peru, have yielded skipjack with gonads in as advanced a state of maturity, even though many fish taken in these localities are of a size (usually over 40 cm.) at which full maturity and spawning are possible. Orange's data are summarized in figure 3, which shows the percentage of females classified as "maturing" for the various areas that contained maturing fish. Orange shows that the offshore insular areas, the Revillagigedos and Cocos Island, have higher percentages of mature females than areas nearer to the coast. A much larger percentage of fish in the Revillagigedos mature above 68 cm. than at smaller lengths, but fish of this size are unusual.

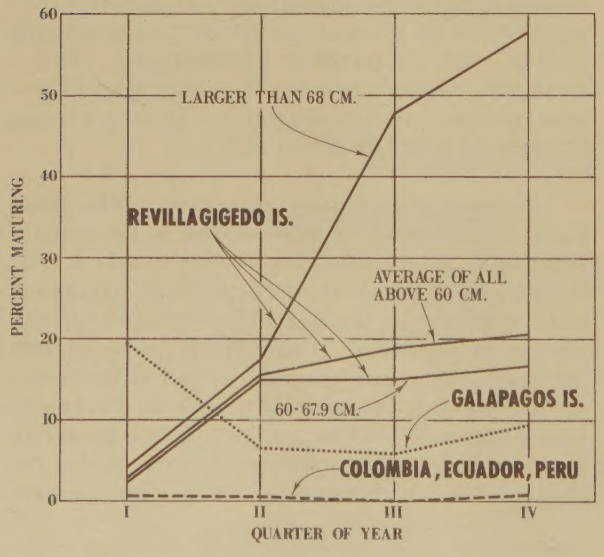


Figure 3.--Percentage of females classified as maturing during each quarter of the year from various areas of the eastern Pacific. (Data are from Orange, 1961.)

The Revillagigedo area also is unique in that it exhibits a peak incidence of maturity during the second, third, and fourth quarters, whereas all the other areas considered by Orange (coasts of Mexico, Central America, Colombia, Ecuador, Galápagos, and Cocos Island) show tendencies toward winter maturity.

As Orange (1961) points out, the minimum size at which "spawning" occurs in the Revillagigedos is 55 cm., which is smaller than some of the fish found in a condition of latent maturity in the Baja California fishery. Orange's use of the word "spawning" is unfortunate, because the developing gonads described by him were not in such an advanced state as to be considered per se indicators of imminent spawning; the amount of time required for these fish to become running ripe is not known.

The concept that skipjack in imminent spawning condition are unavailable to the usual methods of capture in any of the fisheries operating in the spawning areas is based on the difference in ova diameters: between ova of running ripe skipjack which are rarely taken, and those of fish with mature but not running ripe gonads. Brock (1954: p. 100), for example, points out that the larger ova from maturing skipjack taken in the Hawaiian fishery range between 0.4 and 0.9 mm. in diameter with an average maximum modal size of 0.7 mm. He indicates, however, that the single running ripe skipjack that was available for his examination had ova with an average diameter of 1.125 mm. Brock's observations on mature ova diameter concur with those of Raju (1963) and Bũnag (1956). Brock's observations on ova diameter from running ripe skipjack concur with Yoshida[3/]. The time interval required for a 0.7 mm. skipjack ovum--which is 60 percent of the attainable spawning diameter or 20 percent of the attainable spawning volume--to reach extrusion size is unknown. The possibility that small fractions of the total skipjack egg complement become ripe and are extruded over long periods of time seems contrary to Brock's observation of a ripe female where "...a gelatinous mass of eggs came foaming out of the visceral cavity in sufficient quantity to make a fair double handful." It thus is evident that skipjack are unavailable to the usual methods of capture for some interval prior to their spawning.

3/ Yoshida, Howard O. Skipjack tuna spawning in the Marquesas Islands and Tuamotu Archipelago. Bureau of Commercial Fisheries Biological Laboratory, Honolulu. (In press.)

Length-Frequency Distributions of Hawaii Samples

Use of length-frequency distributions to determine age and population structure of skipjack is made difficult by the lack of ancillary aging methods. The problem is further complicated by the skipjack tuna's presumably extensive migrations and by fluctuations in availability which suggest that the length-frequency distributions may not be representative of the populations that are sampled.

Length-frequency samples were obtained by systematic sampling from Hawaiian skipjack landings during various months from 1948 to 1954 and again from 1959 to 1963. For economy of space, data for 1952-63 only are presented in figure 4 as percent frequency. These percent frequencies are based on many samples and measurements for most months, so chance fluctuations are likely to be small. These frequencies are intended to show the size distribution of skipjack for each month and should not be construed as representing the relative magnitudes of the catches among the various months.

An examination of the length-frequency distributions shows that during the winter three dominant modal groups may be evident. Although during the summer there are typically two modal groups, on occasions such as in August 1959 and June 1961, three were noted. Typical modal lengths for the winter are 35, 50, and 70 cm. (the modal lengths given here and elsewhere in the text, unless specified, give the approximate modal values for these typical groups), while those for

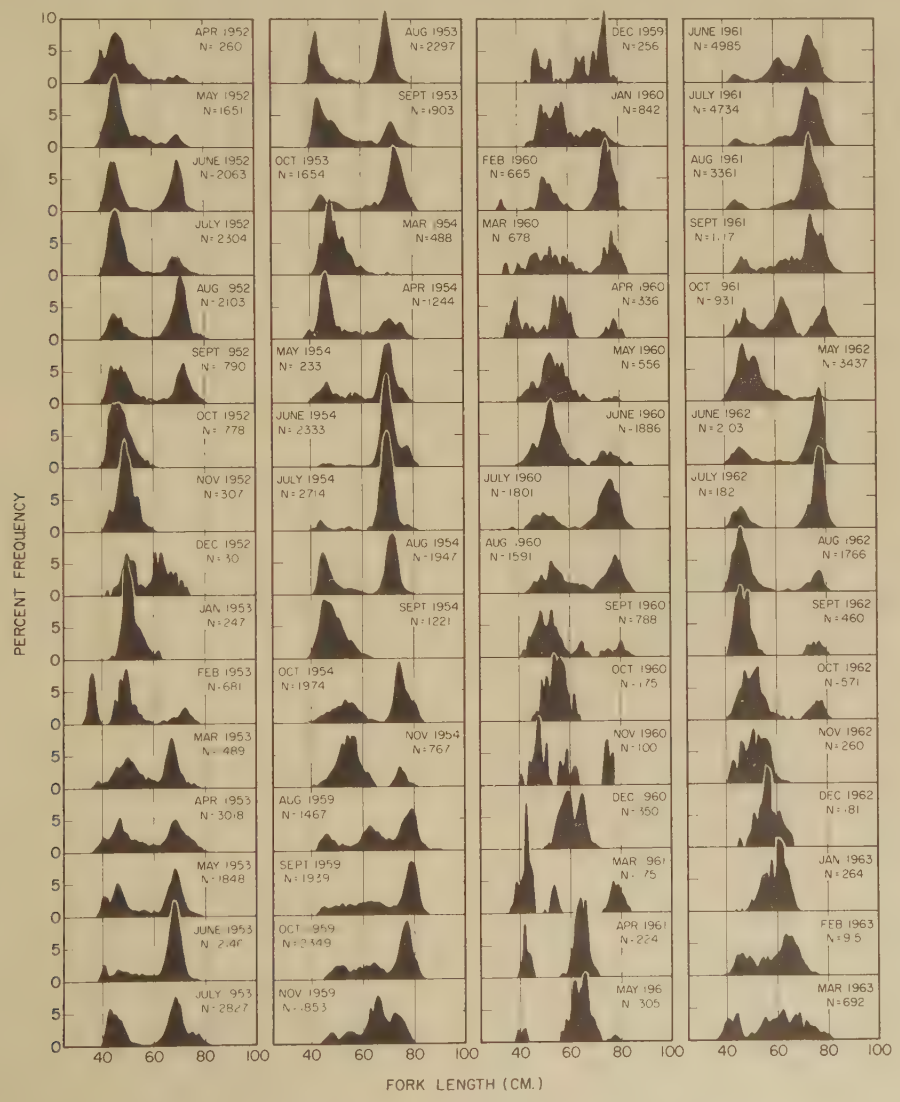


Figure 4.--Percent frequency distributions of skipjack samples caught by the Hawaiian fishery during various months.

the summer typically are 45 and 70 cm. Modes also occur in intermediate positions. The 35-cm. group does not always appear in the catches; the cannery which receives the bulk of the Hawaii catch has established a policy which discourages fishermen from taking fish of this size. The same length-frequency pattern persists for several months in many years; for example, May through July of 1954 showed relatively small proportions of fish smaller than 60 cm., whereas summer samples for 1952 contained relatively large proportions of fish under 60 cm. The consistency of the frequency distributions for some adjacent months is a further suggestion that they are representative of the population as it is sampled by the fishery.

Another interesting feature of the distributions is the occasional occurrence of a modal group in the April-September samples between the 45- and 70-cm. groups. Definite examples of this group are found, for instance, in the August 1959 distributions. This intermediate group also is evident in a less pronounced degree in other summer samples. The occurrence of this group probably is not due to chance because the samples are large and the group is evident in some cases for at least 2 months.

Modal sizes.--The modal sizes for the dominant modal groups were determined from length-frequency distributions (fig. 4). The determination of which modal groups were dominant was subjective but based on a conservative criterion because only prominent modes well separated from one another were selected to the exclusion of minor irregularities in the frequency profile. These selected modal points were plotted in figure 5 for each month and year for which data were available. It should be emphasized that other modal groups are evident and probably real, but they were not considered dominant and are therefore not included in figure 5.

Several characteristics of figure 5 are evident. Most months contain two modes, other months three or four modes. Certain years (e.g., 1950, 1959) have typically three modes for many months. The intermediate mode (about 60 cm.) is most common during the nonsummer months.

The positions of the modes occur at about 45 cm., 60 cm., and 70 cm. Modal lengths for the 45-cm. group, which is presumed to be the fastest growing of the various modal groups, do not necessarily increase with time; in fact there are some months when the modal length stays the same or even decreases. There is a tendency for modal lengths to follow a U-shaped curve with a minimum in length occurring during the summer. The lengths of the 70-cm. group seem to have no consistent pattern except that there has been a trend in some years for these fish to increase in size. It is evident that the month-to-month change of modal sizes in many instances cannot be representative of growth; these data suggest passage of successive groups through the fishery. The varying rate of change in modal length suggests that this passage is not uniform with respect to time.

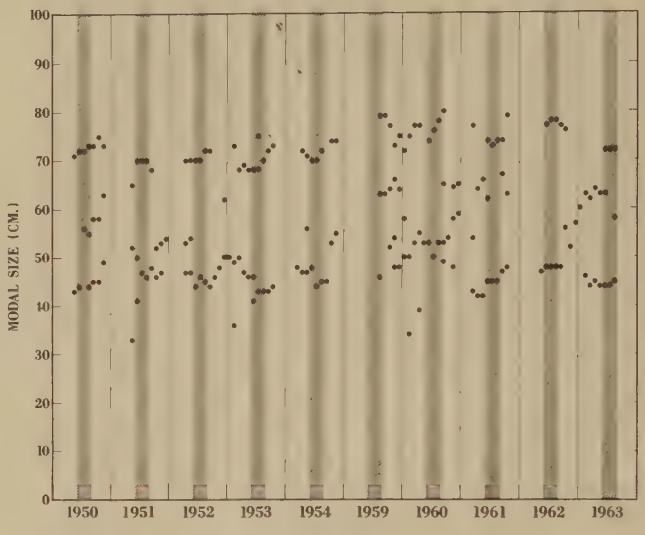
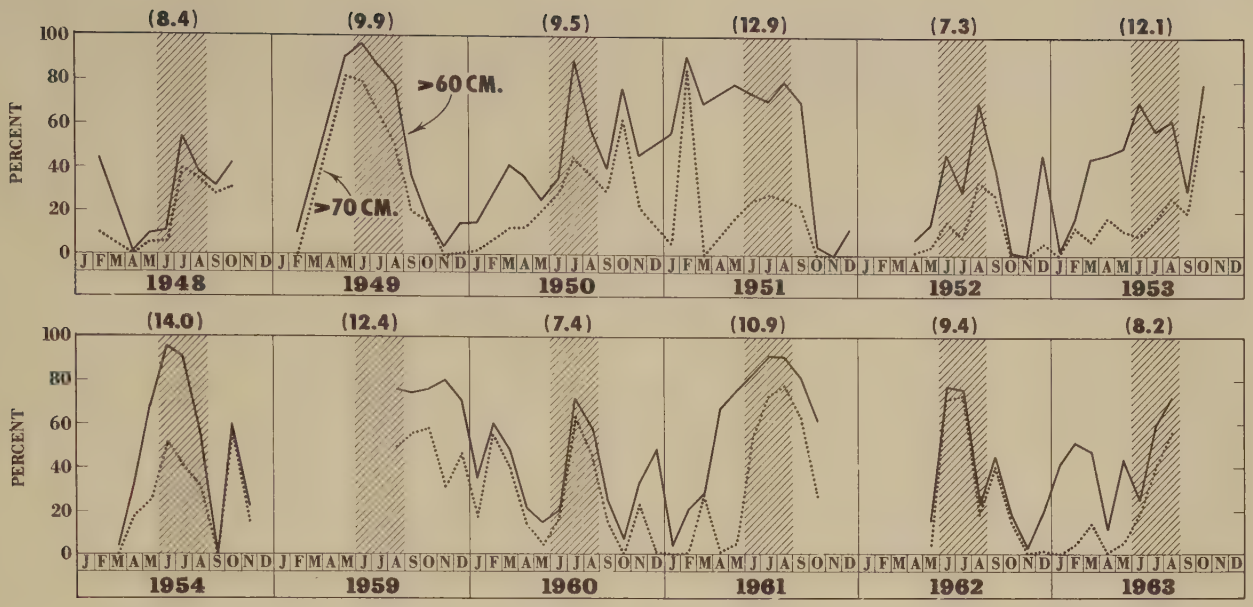


Figure 5.--Size distribution of dominant modes in the length-frequency samples of skipjack taken during various months from the Hawaiian fishery. The shaded portion shows the summer peak fishing period.

Size distribution.--The proportions of skipjack in the length frequencies (fig. 4) over 60 and 70 cm. are plotted in figure 6. The proportion of skipjack over 60 cm. is shown invariably to exceed the 50th percentile during the summer. The total yearly catch is weighted toward summer catches, since a large proportion of the total landings is taken during the summer. Skipjack larger than 60 cm. are often less available in the presummer and postsummer periods. Occasionally fish larger than 60 cm. reach a peak in availability in December, January, or February; this peak occurs most often near February.

Proportions of fish larger than 70 cm. also are plotted in figure 6, and they likewise show a peak for most summer months. In some years, such as 1960, the proportion of fish over 60 cm. is a fairly close parallel to the proportion of fish over 70 cm. In other years, such as 1951, 1953, 1954, and 1959, there are relatively large deviations between the proportions of fish over 60 and 70 cm.; in these years the commercial catch was relatively large, indicating that the peak


(8.4)
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(9.5)
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1954
1959
1960
1961
1962
1963

Figure 6.--Proportions of skipjack greater than 60 and 70 cm. long, from the length-frequency samples taken during various months by the Hawaiian fishery. Total catch in millions of pounds accompanies each panel. The shaded portion shows the summer peak fishing period.

catches are correlated with relatively high proportions of fish between 60 and 70 cm. The occasional influx of large fish during the nonsummer period consists of fish larger than 70 cm.

Length-Frequency Distributions of Eastern Pacific Samples

Length-frequency distributions for various regions in the northern-eastern Pacific fishery area, compiled by quarter years, are available in Broadhead and Barrett (1964). The most complete set of these data is from the coastal area of Baja California and the Revillagigedo area. These quarterly length-frequencies have been superimposed for each year in figure 7.

Figure 7 shows that an increase in size is not always evident from quarter to quarter; size may decrease, remain stable, or increase from one quarter to the next. A decrease in size during a subsequent quarter-year can be interpreted as an influx of smaller size fish replacing the larger fish of the previous quarter or the removal of the latter by emigration or mortality. Stability in size could be interpreted as a lack of growth, a balance of growth and removal of fish as they become larger, or a constant replacement of one group by another of equivalent size in any one quarter. An increase in size between quarters may be due to growth of the present inhabitants of an area, to the influx of large fish, or the replacement of smaller size fish by larger size fish.

The data of figure 7 were examined to determine the nature of the predominant shift in size between quarters. The between-quarter differences in size were classified either as an increase, a stability, or a decrease in size. These classifications, which, of course, are subjective, are presented in table 1. They show that increases occur less frequently than decreases or stability. Many of the increases occur between the third and fourth quarters. The Baja California samples have more increases.

A pattern seems evident for the Baja California samples in that the fewest increases in size occur between the second and third quarters. Also for some sets of years, the fourth-quarter size distribution seems related to the first-quarter size distribution of the next subsequent year. Furthermore, the data tend to indicate that the sizes are more similar within years, particularly for the second, third, and fourth quarters, than between years.

There are also differences in skipjack size among the areas of the eastern Pacific. Broadhead and Barrett (1964) show that small skipjack (modal length < 50 cm.) are predominant in the Baja California area, large fish (modal size > 60 cm.) are most common in the Gulf of California and the Mexican coast at least in the first quarter of the year, and finally fish of intermediate size are found in the Revillagigedo area. However, the size composition of the Revillagigedo samples has shifted relative to the Baja California samples. From 1958 to 1960 the sizes

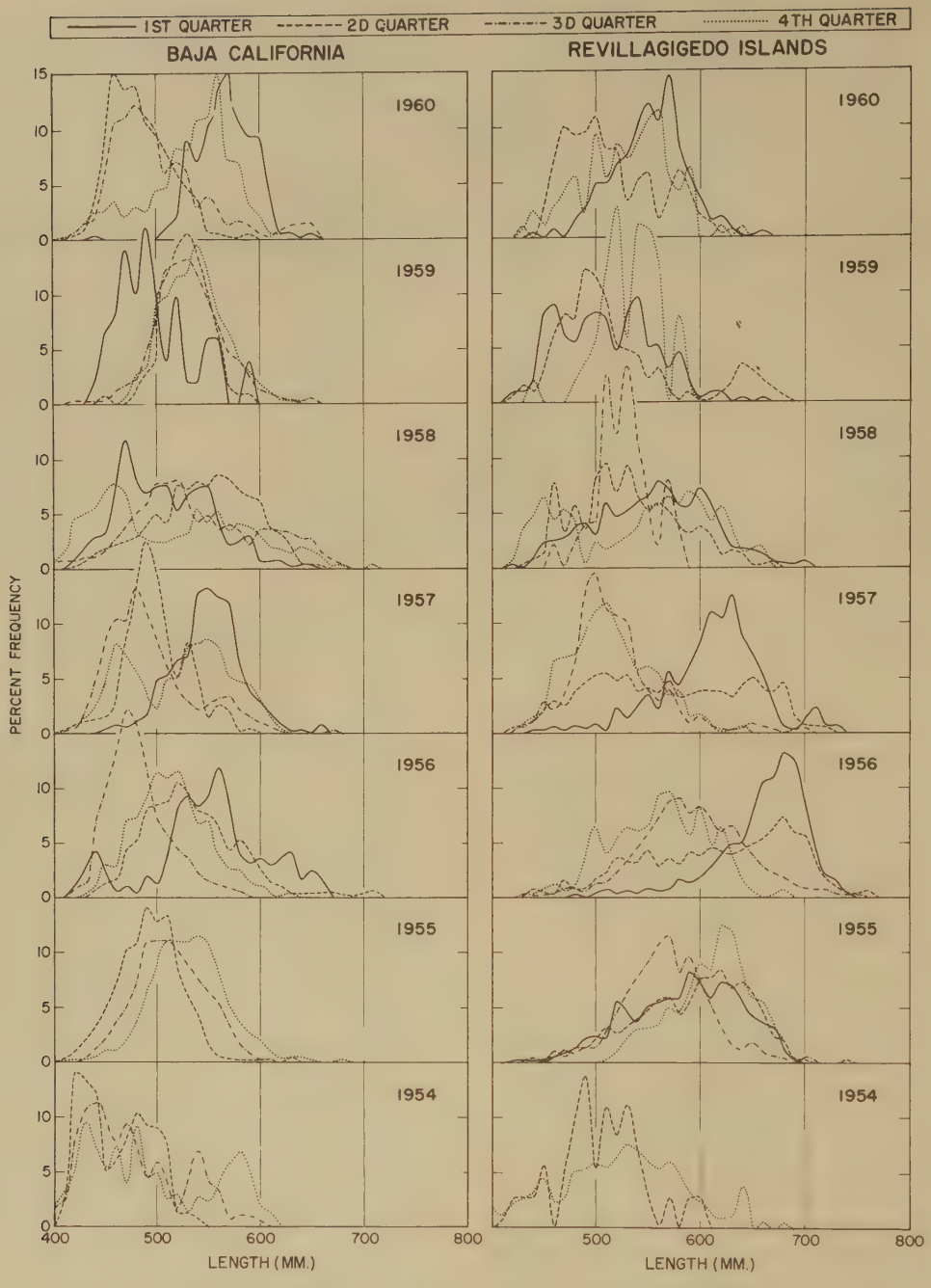

Figure 7.--Superimposition of quarter-year length-frequency distributions of skipjack taken in the Baja California and Revillagigedo regions of the eastern Pacific during 1954-60. Data are from Broadhead and Barrett (1964).

of the Revillagigedo and the Baja California skipjack are about the same. From 1955 to 1957 the Baja California fish are generally smaller than those from Revillagigedo. It seems that the disappearance of the size differential is due to a decrease in the size of the Revillagigedo fish rather than to an increase in the size of Baja California fish.

Comparison of Eastern and Central Pacific Length-Frequencies

A comparison between the sizes of skipjack taken in Hawaiian waters and those from the eastern Pacific is also of interest. Data for various regions of the northern area of the eastern Pacific arranged by quarters are available in Broadhead and Barrett (1964). Data from both

Table 1.--Between quarter increases in size (+) and stability or decreases in size (-) for major portion of skipjack length distributions sampled from fish taken in the Baja California and Revillagigedo region of the eastern Pacific. Blank spaces indicate no data. These changes in size are interpreted from data presented by Broadhead and Barrett (1964)

Year	1954				1955				1956				1957				1958				1959				1960			
Quarters	1-2	2-3	3-4	4-1	1-2	2-3	3-4	4-1	1-2	2-3	3-4	4-1	1-2	2-3	3-4	4-1	1-2	2-3	3-4	4-1	1-2	2-3	3-4	4-1	1-2	2-3	3-4	4-1
Baja California		-	-			+	+	+	-	-	+	+	-	-	+	-	+	-	-		+	-	-	+	-	-	+	
Revillagigedo Islands				+	-	-	+	+	-	-	-	+	-	-	-	+	-	-	+	-	-			+	-			

the eastern Pacific and Hawaiian fisheries for only 3 years (1954, 1959, 1960) have been published. As previously noted the most complete set of data from the eastern Pacific is from Baja California and Revillagigedo samples. Since the fairly consistent relationship of sizes between areas of the northern-eastern Pacific already has been indicated, it will suffice to compare the Baja California size distribution with that of the Hawaiian fishery. To place the material on a comparable basis with that of the eastern Pacific, the Hawaiian data have been compiled by quarter-years and plotted on an increased scale (fig. 8). These composite curves are, of course, weighted by the number of fish in each size for each month or subregion included in the sample. The large number of samples and measurements suggests that the curves are fairly representative of lengths in the population for the considered time period and that they have an accuracy suitable to illustrate the points to be discussed.

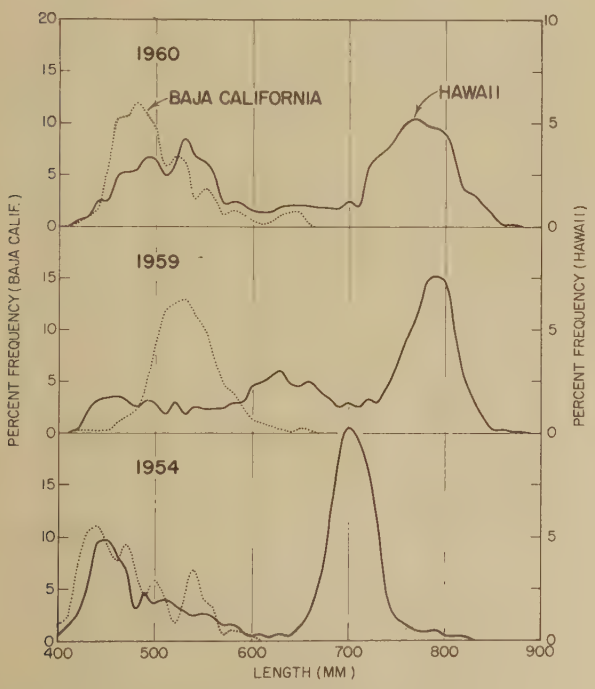

Figure 8.--Length-frequency distributions of skipjack taken during the third quarter of the year from fisheries off Baja California and the Hawaiian Islands. Note that the Hawaiian length-frequencies are plotted on an increased scale. Data on Baja California samples are taken from Broadhead and Barrett (1964).

In general the curves for the Hawaiian samples are bimodal; those for the Baja California samples for the most part have a single mode. The connotations of unimodal and bimodal, in this case, refer to the general appearance of the curves and are not intended to exclude the possibility of more than one modal group within a particular mode.

Discrepancies in the length-frequency distributions, during the various quarters, between Hawaiian and Baja California samples may be attributed to a variety of causes. Some of these causes are probably related to differences in the time sequence--between Hawaii and the eastern Pacific--of the previously mentioned phenomena which affect stability in size (i.e., balances among growth, immigration, and emigration). Of particular interest are the third quarter length-frequencies because these generally reflect peak catches in the Hawaiian and eastern Pacific. It is likely that they, more than the samples at other times of the year, most accurately represent the total population.

The data for 1960 and 1954 show remarkable similarities between the eastern Pacific and the small-size Hawaiian fish. The minimum sizes of fish from both fisheries are about the same, and their distributions appear to have several parallelisms in frequency. The 1959 distributions are, however, quite different. It would seem, at least in some years, that the Hawaiian and Baja California-Revillagigedo fish have common elements in size-frequency distribution.

Movements

This section considers skipjack movements as inferred from tagging studies conducted by the IATTC. These studies have yielded many short distance recoveries and a total, to date, of three midocean recoveries.

Tagging in the eastern Pacific.--Most skipjack tagging in the eastern Pacific has been undertaken by the IATTC. Tag recoveries from skipjack tagged in the eastern Pacific show essentially two patterns of movement: a pattern that seems typical for skipjack tagged to the north of the Gulf of Tehuantepec and another pattern for those to the south of this area. Interchange of tagged fish in the north-south direction across the Gulf of Tehuantepec (lat. 15° N.) has not yet been reported.

In the northern region, studies by the California Division of Fish and Game (Blunt and Messersmith, 1960) have indicated, with limited data, that there is northward movement of skipjack in May and June, northward and southward movement in July, and southerly movement in September. Schaefer, Chatwin, and Broadhead (1961), with large numbers of tag returns, have shown there are essentially no interarea movements among the IATTC statistical areas north of the Gulf of Tehuantepec.

In the southern region, there appears to be relatively greater coastwise movement than in the northern region. Blunt and Messersmith (1960) have shown interchange between the Fourteen Fathom Bank (long. 80° W., lat. 9° S.) and the Gulf of Guayaquil (long. 80° W., lat. 3° S.). More detailed studies by IATTC (Schaefer et al., 1961) have shown interchange among the regions off Colombia, Ecuador, and Peru. The fish seemed to move toward the Fourteen Fathom Bank in the summer and away from it in the winter. These authors also give data which indicate that skipjack marked off Central America may be recovered in South American fisheries.

Long distance tag recoveries.--To date three eastern Pacific tagged skipjack have been recovered in the central Pacific (fig. 9). The two recoveries in Hawaiian waters were of fish tagged in the spring and fall. The skipjack recovered in equatorial waters was tagged in the winter, was at large for a shorter period of time, and was smaller than the two tagged fish recovered in Hawaiian waters.

These three recoveries present problems of interpretation. How valid are inferences regarding the movements of large numbers of fish based on a few tag returns? To provide some tangibility for this question, the probabilities of recovering a skipjack from a region different from that in which it was tagged should be considered. This, however, requires a discussion of various satellite problems such as the distribution of fishing effort on tagged fish, tagging mortalities, the distribution of tagged fish among untagged fish, etc. Many aspects of these problems have been discussed in IATTC publications (e.g., Schaefer et al., 1961, Barrett and Connor, 1962). I cannot evaluate all aspects of these problems. Furthermore, many of the data necessary for such an evaluation are unattainable with available techniques. Therefore, in this study, the probabilities of capturing a tagged interregional-migrant skipjack can only be appraised in a gross and qualitative fashion.

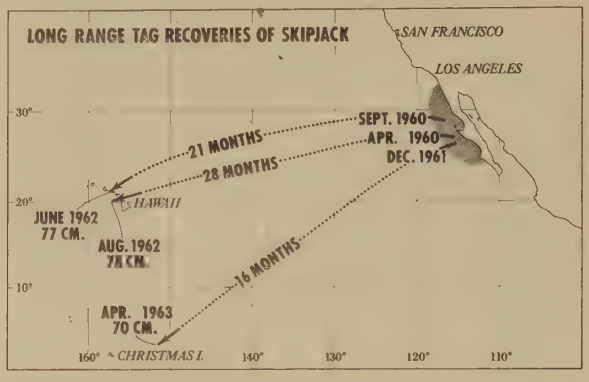

Figure 9.--Schematic representation of three long-distance recoveries of tagged skipjack showing time of tagging, time out, time of recovery, and size. These fish were tagged by IATTC.

The likelihood of recovering a tagged interregional-migrant skipjack is dependent on, among other things, the amount of effective fishing effort expended for skipjack in the region of potential recapture. A fairly intensive (for the central Pacific) skipjack fishery exists in the immediate vicinity of the Hawaiian Islands; in other areas of the central Pacific, however, relatively few skipjack are taken. Therefore, the recovery of an eastern Pacific tagged skipjack in the equatorial central Pacific may appear more likely to represent a large movement of fish than the two Hawaii recoveries. Of the several thousand skipjack tagged in Hawaiian waters during 1957 and 1958 none have been recovered in the eastern Pacific fishery.

Prediction of Hawaiian Skipjack Catch

Seckel and Waldron (1960) have derived an index which predicts the magnitude of the annual catch of skipjack tuna in the Hawaiian fishery. In essence it forecasts the magnitude of the summer catch (June, July, and August) because a considerable proportion of the Hawaiian catch is taken during the summer. The index itself is based on the time during January, February, or March when the sea-surface temperature off Oahu, Hawaii, changes from cooling to warming. The prediction states that the annual skipjack catch will be above average when the shift from

cooling to warming occurs early in the January-February-March period; when this shift is late in the period catches will be below average.

The quality of the predictive index bears an important relation to the biology of the skipjack. For example, if the time of warming index accounts for a high degree of variability in catch (in the Hawaiian fishery, catch is closely correlated with catch-per-unit-of-effort, R. Uchida, personal communication), then variations in catch are probably related to features of the environment that operate not more than several months prior to the summer peak fishing period. If this is the case it is unlikely that year class strength, for example, would affect the catch since year class strength of the fishable stock is probably fixed at least several months prior to the period of peak fishing. As the degree of variability in catch, accounted for by its regression on time of warming, is decreased, the possible operation several months prior to the summer peak fishing period of mechanisms unrelated to the time of warming become increasingly apparent.

It seemed that a statistical evaluation of the relation between sea-surface warming time and skipjack catch would be appropriate. For this analysis sea-surface temperatures taken about every other week off Koko Head, Hawaii, were used. Least squares parabolas were fitted to the temperature curves for the period between December 1 and May 31 for the years for which data were available (1956-63). The time of shift from cooling to warming was obtained by taking the first derivative of each parabola, setting the derivative equal to zero, and solving to obtain the minimum temperature. The point on the abscissa where temperature is at a minimum is, of course, the time of shift from cooling to warming.

The correlation coefficient between time of warming and total catch was 0.664, which is non-significant at the 5-percent level with six degrees of freedom. This neither confirms nor denies the existence of this relation, but if a relation does exist the available degrees of freedom are not sufficient to demonstrate significance. Let us assume, however, that two more degrees of freedom are acquired and that the relation is adjudged significant with a correlation coefficient of 0.664. We would then say that 44 percent of the variation in catch is accounted for by time of warming; the other 56 percent is unexplained and could be due to events which are uncorrelated with time of warming such as inter alia year class strength and size of fish.

Subpopulations

Evidence for the existence of subpopulations of skipjack in the Pacific has been advanced by Sprague and Holloway (1962) and Sprague, Holloway and Nakashima (1963). This evidence is based on the existence of immunogenetically separable groups of skipjack. The location of these subpopulations is charted by Sprague (1963). His figure shows two subpopulations (I and II) in the Hawaiian region, one (III) in the equatorial region, three in the South Pacific (IV, V, VI), and one (VII) in Micronesia. A cursory examination of subpopulation data shows no grossly apparent relation between subpopulations I and II and size of fish and time of year for the Hawaiian samples. Attention is called to Hennemuth's (1959) paper which shows morphometric differences in skipjack among areas within and between the eastern and central Pacific.

HYPOTHESES

In this section the material on spawning, size distribution, movements, and gonad indices is synthesized into a set of hypotheses concerning the origin of the skipjack exploited in the eastern Pacific, their mode of entrance into the eastern Pacific, the variables associated with their departure from the eastern Pacific, and the origin of the fish exploited in Hawaii. I am not the first to present some of the ideas on which these hypotheses are based, viz., "...it appears that some of the west coast population [of skipjack] range far to the westward" (Schaefer, 1963: p. 50) and "these [tag] recoveries are strong support for the hypothesis, which we have frequently mentioned, that the skipjack of the eastern Pacific may undertake long offshore-inshore migrations" (Schaefer, 1963: p. 57). These allusions are similar in spirit to some of the hypotheses entertained in this paper, but it will be seen that they are somewhat different in concept.

The phenomena which the hypotheses of this paper attempt to account for are undoubtedly complex, and for this reason I suspect that in some cases the explanations offered are oversimplifications. I hope that the simplified picture presented here will generate further questions on the biology of the skipjack tuna.

Skipjack Exploited in Eastern Pacific

It appears as though skipjack tuna that are taken in the eastern Pacific Ocean are generated from spawnings in the central Pacific Ocean. This concept is based on the distribution of skipjack larvae, which indicates apparently negligible spawning (relative to the numbers of skipjack

spawned in the central Pacific) to the east of about long. 120° W. It could be asserted that this negligible spawning in the eastern Pacific, nevertheless, contributes a large recruitment to the eastern Pacific fishery. This, however, seems unlikely; therefore, I conclude that those skipjack taken in the eastern Pacific fisheries are immigrants from the central Pacific. The size of skipjack that immigrate into the eastern Pacific is not certain, but some of the fish may weigh less than 4 pounds (Schaefer 1961: p. 67-69).

A consideration of skipjack tuna in the central Pacific suggests that these fish do not comprise a single, homogeneous, population unit. This suggestion is derived from at least two lines of evidence. First, immunogenetic studies by Sprague (1963) demonstrate the existence of several subpopulations in the central Pacific. Secondly, a cursory examination of the distribution of skipjack larvae shows their densities are not uniformly distributed in space or time throughout the central Pacific. The lack of uniformity suggests the existence of potential isolating mechanisms or the possibility of several spawning groups implying the existence of several subpopulations.

Despite a poor definition of the mechanisms that isolate the various subpopulations of skipjack in the central Pacific, the spatial-temporal distribution of larvae and the results of immunogenetic studies suggest that the central Pacific can be considered, from a hypothetical point of view, to consist of three possible zones of origin for those apparently adolescent skipjack caught in the northern- and southern-eastern Pacific fisheries. These, in a very broad sense, are the Hawaiian Zone, the Line Islands or Equatorial Zone, and the Marquesas Zone.

Our consideration of the origin of those skipjack caught in the eastern Pacific will be limited to the Hawaiian and Equatorial Zones. This limitation results from the speculation that large numbers of fish from the Marquesas Zone do not enter the eastern Pacific fishery area. (The speculation is perhaps more likely for skipjack that originate in the Tuamotus than for skipjack that originate in the Marquesas Islands per se.) Three observations support the speculation. First it is likely that those skipjack in the Southern Hemisphere exhibit the same apparent tendency toward net south-poleward movement (which would reach maximum southward limits in the northern winter) as is found for the apparently net north-poleward movement in the Northern Hemisphere. In order for Marquesas Zone skipjack to enter the Central and South American fishery areas they would have to exhibit at least a slight northern component in movement and this seems unlikely for large numbers of these fish. The second observation concerns reports of extremely large skipjack taken in the Society Islands. Since these reports had not been verified an attempt was made to secure some length-frequency distributions from Tahiti. Thirty-three lengths were obtained. These lengths were compared with 125,105 length measurements made during the last several years on samples from the Hawaiian fishery. Only in an extremely minute possibility could the Tahitian and Hawaiian samples be drawn from the same population of lengths. The Tahitian sample contained fish several centimeters, on the average, larger than the Hawaiian samples. This could result from a variety of phenomena. One possibility is that the Tahitian fish are unexploited relative to the Hawaiian fish. I will postulate later in this paper that large components of the Hawaiian fish do not originate in the Hawaiian Islands, but elsewhere--probably in the equatorial central Pacific. Now, if the Hawaiian lengths are representative of equatorial central Pacific lengths then it could be inferred that the Tahitian or Marquesas Zone fish are fished to a less degree than the Hawaiian component of central Pacific fish. Depending on the relative magnitudes of fishing intensity and stock sizes etc., this might indicate that the Marquesas fish do not enter the eastern Pacific. Thirdly, it is again noted that skipjack in the Marquesas Zone comprise different subpopulation(s) than those of the rest of the central Pacific and, while it is not necessary, it is likely that their migratory behavior is different than the subpopulation(s) to the north. If it is different and the subpopulation(s) to the north enter the eastern Pacific, then the subpopulation(s) of the Marquesas Zone do not. These three observations then, taken together, have generated the speculation concerning the Marquesas Zone fish.

Since, by hypothesis, the Marquesas Zone does not contribute significant numbers of individuals to the skipjack taken in the eastern Pacific, it becomes appropriate to examine the relative likelihoods of Hawaiian or Equatorial Zones as points of their origin for the eastern Pacific skipjack. These likelihoods are reckoned from inferences drawn from composite length-frequency distributions, changes in length-frequency distribution and gonad maturity within the eastern Pacific fishery areas, and from tagging studies.

A first inference concerning the origin of eastern Pacific skipjack is based on the spawning destination of eastern Pacific emigrants. If it can be established that emigration is associated

with spawning, then the destination of the spawning subpopulations should, on the average, be coincident with the zone of their natality. The concept of spawning-associated emigration of eastern Pacific fish is based on the relative immaturity of skipjack in the eastern Pacific, an apparent reduction in the number of larger skipjack in the eastern Pacific fishery, the fact that the onset of advanced maturity in the eastern Pacific area is correlated with attainment of large size, an incidence of more nearly mature fish near the offshore islands than near the American coasts, and an apparently negligible spawning in the eastern Pacific.

As for their spawning destination it is perhaps significant that skipjack at the northern and southern extremes of their range in the eastern Pacific have gonads in a resting stage of maturity. Also, there is a tendency toward an extensive period of summer maturity in the Revillagigedos and winter maturity south of the Revillagigedos to Cocos Island. This implies that, depending on the time interval from an advanced stage of maturity to spawning, skipjack in the Revillagigedos spawn well into the fall. As the time of spawning proceeds from summer through fall to winter, the northern limit of this activity in the central Pacific moves south. In other words, in the northern fall there is a tendency toward more equatorward spawning than Hawaiian-Zone spawning. For the winter-maturing fish south of the Revillagigedos, spawning must take place south of or in the Equatorial Zone, because there is almost no winter spawning in the Hawaiian Zone (Brock, 1954, indicates that Hawaiian-Zone spawning ends in September). Skipjack south of the Revillagigedos to Cocos Island, however, are less mature than those near the Revillagigedos proper. This might indicate a northward movement of skipjack along the southern Mexican coast, but tagging data have shown little interchange between these areas. Furthermore, those found north of the Gulf of Tehuantepec in the eastern Pacific may be composed of two contingents: one contingent exhibits summer maturity and may spawn in the Hawaiian or Equatorial Zone; the other exhibits winter maturity and spawns at least as far south as the Equatorial Zone.

A second inference, relating to the size distribution of skipjack which immigrate into the eastern Pacific, is based on the observation that Baja California and Revillagigedo length-frequency samples often show no marked increase in length over several months. If compensatory or differential growth does not operate, then these fish must have been spawned over several months. Since the predominant spawning period in Hawaiian waters is less than several months the Baja California and Revillagigedo fish must contain a component which is of non-Hawaiian origin. It seems likely that this component originates in the equatorial region. A degree of caution should be retained, however, in considering the three-quarter year size replacement and the gonad maturity indices because these indices might reflect phenomena that represent relatively few fish at either extreme of the three-quarter year period.

A third inference concerns the observation that size distributions of skipjack taken in the third quarter of the year in the northern-eastern Pacific fishery often exhibit a size component slightly larger or smaller than the small-size modal group of Hawaiian fish. If these differences are not due to sampling errors, then they might arise from several possibilities. These might include variations in growth rate, slight differences in age (of the order of a few months), and size specific movements. While there is no strong evidence to support any of these possibilities, the size range of any "year class" (barring compensatory growth) from equatorial waters would be expected to have more larger and smaller elements than a "year class" generated in Hawaiian waters because of the more extended period of spawning in equatorial waters.

A final inference concerning the relative merits of either the Hawaiian or Equatorial Zone as a place of birth for the skipjack harvested in the eastern Pacific is based on the three mid-Pacific tag recoveries that resulted from extensive tagging in the eastern Pacific. Although it is difficult to place a great amount of weight on three tag recoveries, it can be indicated that if skipjack emigrating from the eastern Pacific all enter the Hawaiian Zone, then a greater number of tag returns should be obtained from the Hawaiian Islands. The pattern of recoveries, considering the location of fishing effort, is not inconsistent with the hypothesis that the major movement of skipjack in the northeastern portion of the Pacific is usually between the equatorial central Pacific and the Baja California region.

As mentioned previously a segment of the equatorial fish, potential recruits to the eastern Pacific fishery, disperses to the east and north. As the fish move east they are "split" into a northern group that enters the Mexican fishery area and a southern group that enters the South American fishery area. The mechanisms by which the skipjack are split into northern and southern contingents may be manifold and probably are not fixed in time or space. The extent to which the mechanisms partition skipjack into

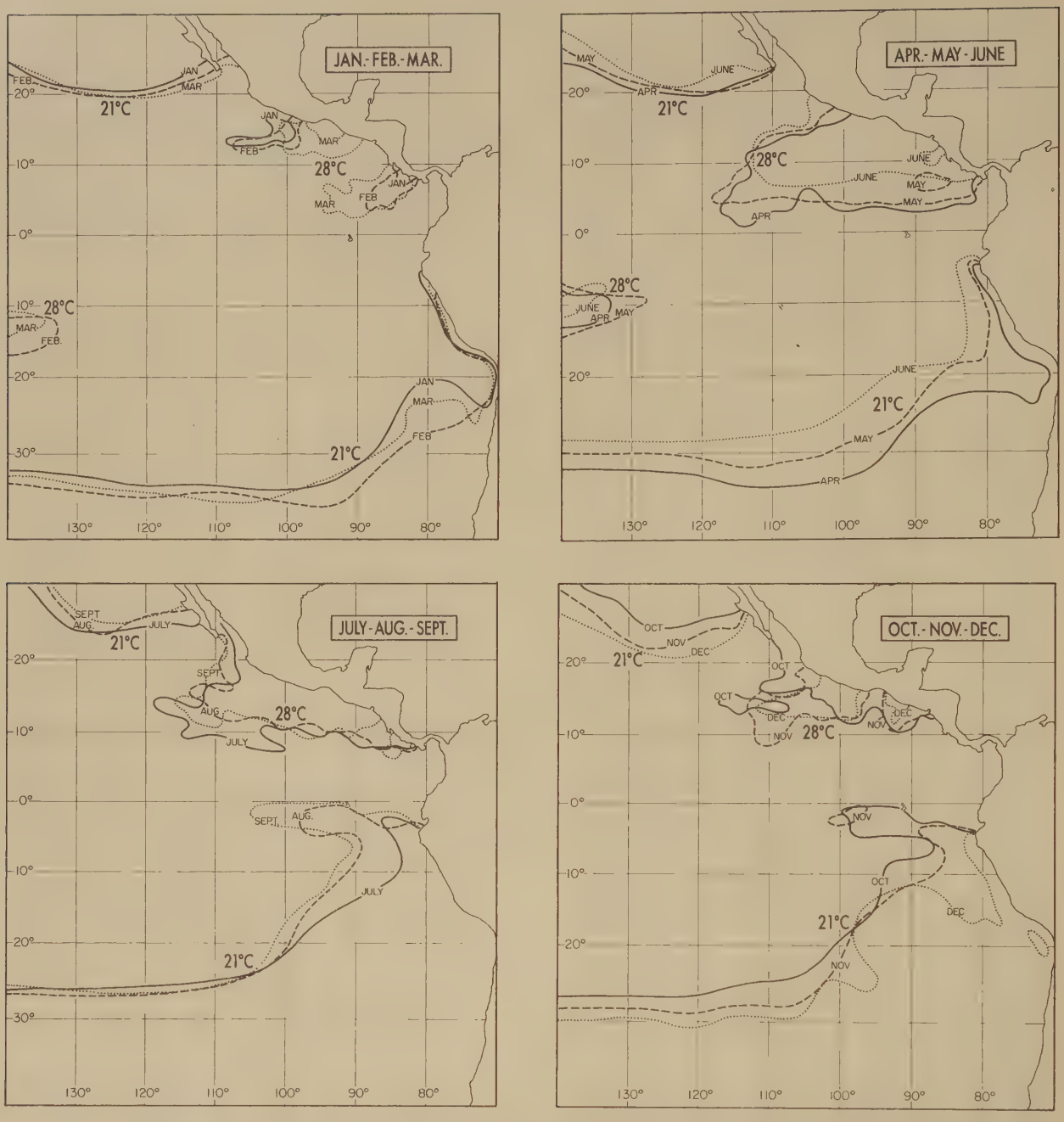

Figure 10.--Location of 21° and 28° isotherms in the eastern Pacific according to Wyrtki (in press). Blackburn (1962) has suggested that the distribution of skipjack harvested along the coasts of the Americas is coincident with surface temperatures between 21° and 28° centigrade.

northern and southern contingents is a function of the north-south and temporal distribution of eastward-moving skipjack as these fish encounter the splitting mechanisms. One possible splitting mechanism is the warm water cell (surface temperature greater than 28° C.) in the vicinity of lat. 15° N. off the coast of Central America. The location of this warm water cell for average conditions is contained in Wyrtki's[4/] recent paper (see fig. 10) and has been discussed by Blackburn (1962: p. 39-40), who suggested that it impedes north-south movement of skipjack across lat. 15° N. to an extent which varies with surface temperature. This is undoubtedly the case, but it appears that the cell has a more important effect; it is one of the mechanisms that serve to split skipjack into northern and southern groups.

4/ Wyrtki, Klaus. Thermal structure of the eastern Pacific Ocean. Deut. Hydrograph. Z. (In press.)

Skipjack Taken in Hawaiian Waters

The Hawaiian skipjack fishery uses pole-and-line gear and live bait. The average annual catch is about 10 million pounds, fluctuating in recent years between 7 and 14 million pounds. The bulk of the catch (usually about 70 percent by weight) is taken during June, July, and August, and generally consists of large numbers of "season-size fish" (>than 60 cm.). "Season-size fish" also occur sporadically during the winter but are not nearly as abundant as during the summer "season." The magnitude of each year's catch has been predicted for several years (Seckel and Waldron, 1960). This prediction is based on changes in sea-surface temperature that occur in February and March and, in essence, foretells the magnitude of the catch during the "season" in June, July, and August. Several problems arise in interpreting the nature of the fluctuations in the Hawaii catch. A consideration of these problems generates several hypotheses pertinent to the origin of those skipjack taken by the Hawaiian fishery.

Skipjack spawn in the Hawaiian Zone so it is likely that at least some of the skipjack caught in the Hawaiian Zone fishery are generated in this Hawaiian Zone. Immunogenetic studies have shown that those skipjack caught in the Hawaiian Zone fishery are comprised of two subpopulations. On this basis I postulate that at least one of these two subpopulations has its origin in the Hawaiian Zone. The other subpopulations may or may not originate in the Hawaiian Zone, but in any event the two subpopulations must maintain a degree of isolation at spawning time.

A wide variety of isolating mechanisms that tend to reduce interbreeding between populations of many organisms are described by various authors (see, for example, the concise résumé by Allee, Emerson, Park, Park, and Schmidt, 1949: p. 606). Some possible isolating mechanisms that could maintain immunogenetic distinctness between two groups of skipjack are distance between spawning units, differences in the time of spawning between breeding units, island association of spawning, island association of relatively high larval survival, length segregation at spawning time, and the association of breeding groups with particular water types. Both distance and time of spawning could operate as isolating mechanisms between the Hawaiian and Marquesas Zones because these Zones are at the extremes of the north-south spawning range; spawning in the Hawaiian Zone occurs predominantly during the northern summer whereas spawning in the Marquesas takes place predominantly during the northern winter. These mechanisms also probably operate between the Hawaiian and Equatorial Zones. Included in the concept of distance as an isolating mechanism is the apparent island-association of spawning or high larval survival, suggested by what appears to be relatively high densities of skipjack around major island groups.

Another possible isolating mechanism is length segregation of skipjack schools (Brock, 1954: p. 98-99). Perhaps at spawning time small differences in length, on the average, may tend to segregate schools of skipjack. Any differences in length between the two populations would act as isolating mechanisms. Since present sampling techniques do not capture skipjack that are spawning or are in an imminent spawning condition this hypothesis cannot be tested. One final type of isolating mechanism involves the hypothesis that subpopulations of skipjack are associated with water types as indicated by temperature and salinity at the sea surface (Sprague, 1963).

Another characteristic of the skipjack taken in the Hawaiian Zone that may indicate a non-Hawaiian origin for some of the fish taken in the Hawaiian fishery is the roughly equal numbers of fish in the 45- and 70-cm. modal group. Catches representative of the full range of sizes for any population should have considerably more fish in the smaller size groups. Several explanations can be offered for the relatively few small fish in the Hawaiian catch. Small fish might not be caught in the Hawaiian pole-and-line fishery; however, there are no data that describe this selectivity. A second possibility is that the large size group of fish contains several age groups indistinguishable with respect to size. This may be partially true, but I believe its extent is insufficient to explain the equal numbers of large and small fish. A third type of selectivity may cause mature fish to be unavailable to pole-and-line gear during the spawning season. The unavailability of imminent spawners already has been pointed out. If the proportion of larger fish in which spawning is imminent is smaller than the proportion of smaller fish in which spawning is imminent, then the numbers of larger fish in the catch will be greater than would be expected if there were no differences in maturation between large and small fish. No data are available on the extent to which imminent spawning affects the representativeness of skipjack samples.

Other mechanisms that might produce relatively large numbers of large fish are the possibility of a disproportionate increase in the density of large fish in the immediate vicinity of the

Hawaiian Islands (i.e., the fishery area) or that equal numbers of large and small fish are produced by an emigration of small fish rather than by an immigration of large fish. The latter possibility is contradicted, however, by the apparently tremendous influx of large fish into the Hawaiian fishery during the summer. If we assumed negligible fishery selectivity and minimal effects of maturity-associated size-specific availability, then the samples indicate there are roughly equal numbers of large and small fish in Hawaiian waters during the summer. This probably is caused by an immigration of large fish that did not originate in the Hawaiian Zone.

Evidence from subpopulation studies and the distribution of skipjack lengths then admit the hypothesis that one of the subpopulations entering the Hawaiian fishery did not originate in the Hawaiian Zone and that this subpopulation is comprised at least, in part, of large numbers of season-size skipjack. As previously noted a prediction has been available for forecasting the magnitude of the annual catch of skipjack in the Hawaiian fishery. A large annual catch is an index of a high apparent abundance of season-size fish. I have shown that certain years with relatively large catches, and thus a high apparent abundance of season fish, were characterized by a reduction in size of the season-size fish. Thus, in years of relatively poor catches the proportion of fish over 60 cm. consists mostly of fish over 70 cm. long (fig. 6). In years of relatively large catches, the season-size fish are mostly between 60 and 70 cm. long and their proportion in the total catch is apparently independent of the proportion of fish over 70 cm. Therefore, since the magnitude of the catch could be predicted and the size distribution is related to the magnitude, the size distribution also could be estimated in the sense that in years of high catch the size of the season-size fish would be slightly reduced.

These predictions imply that the season catch of skipjack is controlled by events that are associated with the warming of the sea surface in the vicinity of Oahu several months before the onset of peak fishing. By this reasoning it would seem that the biomass and size distribution of prerecruits to the Hawaiian fishery are oriented in space and that this orientation is controlled by the absolute position and rate of movement of either the isotherms or properties related to the isotherms.

On the other hand, a study in the degree of variation in the relation between time of warming and catch indicated that a large component of variability in total catch might not be attributable to the sea-surface time of warming index. Therefore, the unexplained variation is due to events other than the time of warming index which is an evident part of the temporal change in sea-surface temperature and occurs a few months prior to each fishing season in the vicinity of Oahu. A possible component of the heretofore unexplained variation is the strength of the various year classes that enter the skipjack fishery. The formation of large or small year classes of the large skipjack taken in the Hawaiian fishery probably takes place 2 or 3 years prior to the recruitment of this large size group and therefore seems independent of events, such as the time of warming, that occur a few months before the fishing season. The hypothesis that year class strength influences the summer apparent abundance of large skipjack is strengthened by the observation that a small-size component of the large-size group becomes particularly evident in years of relatively high catches. It is postulated that this small-size component represents an unusually strong year class. If year class strengths are important components of variability in skipjack catches, then it is also likely that slight reductions in average size of the skipjack during years of high apparent abundance may also reflect density dependent growth that is typical of large year classes for many species of fish.

Additional inferences pertinent to the origin of skipjack taken in the Hawaiian Zone are based on size distribution and growth data from the Hawaiian fishery. Growth of skipjack tuna based on modal progressions within size distributions of Hawaiian samples is often less, on a month-to-month basis, than that estimated from tag returns (Rothschild[5/]). In fact, for some months modes remain the same or decrease in length. These observations suggest that, as in the eastern Pacific, the fishery is constantly being replenished with fish of smaller or equivalent size while at the same time larger fish leave the fishery area. During some years there is a U-shaped distribution of lengths with a minimum in the summer. This could be interpreted as a removal of the larger fish of the small size group during the summer fishery. A second possibility is that smaller fish enter the fishery initially, then emigration is reduced, the ascending right-hand limb of the U-shaped distribution reflecting growth of those that are residual. Thus it is apparent that all exploited subpopulations of skipjack exhibit less than expected increases in length. It is hypothesized that this characteristic is due to certain sizes of fish moving through the fishery.

5/ Rothschild, Brian J. Manuscript. Estimates of skipjack tuna (Katsuwonus pelamis) growth in the Hawaiian Islands. Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

A comparison of length-frequency distributions taken during the third quarter of the year by the Hawaiian and eastern Pacific fishery provides further clues to the origin of skipjack caught in the Hawaiian fishery. A similarity in size distribution exists between the small-size group of Hawaiian and of eastern Pacific fish for 2 of 3 years for which data are available. This similarity in size could be indicative of a common origin for eastern Pacific and the small-size group Hawaiian fish. By hypothesis the eastern Pacific fish originate in the central Pacific; therefore, the concept of a common origin suggests that those taken in Hawaiian waters also originate in the equatorial central Pacific. The lack of apparent similarities between third quarter length-frequencies of Hawaiian and eastern Pacific fish during the third year for which data have been published is interpreted as an environmentally induced failure of equatorial central Pacific skipjack to enter the Hawaiian Zone during this year.

A consideration of various features of the biology of the skipjack taken by the Hawaiian fishery yields no immediately discernible conclusion regarding the origin of those skipjack taken in the Hawaiian Zone. It seems fairly evident, however, that a likely hypothesis would suggest that one of the two subpopulations that enter the Hawaiian fishery originates in equatorial waters of the central Pacific and is comprised of fish that make up the bulk of the season catch. The magnitude of the season catch may be related to the physical environment, but it is likely that dynamic features of the skipjack populations are also important.

CONCLUSIONS

The purposes of the hypotheses presented in this paper were to assemble data pertinent to understanding the movements of skipjack tuna in the central and eastern Pacific and to provide a guide for future studies. The need for more evidence on the problems of the origin and movement of skipjack tuna is evident. The accumulation of this evidence should be based on a consideration of alternative sets of hypotheses, a substantiation of the assertions made in this paper, and the design of critical experiments to test the hypotheses.

In considering sets of hypotheses other than those proposed in this paper it is important to note that the conceptual division of the central Pacific into three zones of origin puts immediate constraint upon the nature of solutions. Should the central Pacific be considered as a single zone (one huge population of skipjack that extends from the Hawaiian Islands in the north to the Tuamotu Archipelago in the south), as two zones (a northern and southern zone, both or only one contributing to the eastern Pacific fishery), or finally as many discrete zones (each contributing variable proportions of fish to the eastern Pacific fishery), then the nature of the hypotheses based on these considerations might be different than that of the three-zone concept. A consideration of these alternatives and several others has, however, continued to suggest that the three-zone approach presented in this paper is most consonant with the evidence as it is now available. When new and pertinent data are acquired, then it is possible that alternatives will be accepted.

Some of the assertions made in this paper need to be substantiated. Perhaps the weakest assertion involves the exclusion of Marquesas Zone fish from the Central and South American fishery area. The temporal-spatial distribution of skipjack larvae certainly needs to be studied more intensively. One of the more perplexing features of the evidence is the large numbers of immunogenetically distinct groups that have been identified. What are the isolating mechanisms?

Finally, which experiments provide critical tests of the hypotheses? In general, studies of larval and juvenile skipjack are indicated since these studies may provide clues to the year class strength phenomena mentioned earlier in this paper, elucidate isolating mechanisms, and provide samples for subpopulation studies. More specifically an experiment to test the hypotheses is based on the definition of a critical area. This critical area lies along a line between the Hawaiian Islands, the Line Islands, the Marquesas Islands, and the Tuamotu Archipelago. Juvenile skipjack (since adult skipjack appear to be unavailable to capture for some interval prior to spawning; samples of juvenile skipjack are more likely to be from a single genetic pool than the adults) should be taken along this critical area, and their immunogenetic affinities determined with already developed reagents. The immunogenetic affinities of the eastern Pacific adolescent skipjack could then be compared with central Pacific samples to determine the loci of their origin. The conduct of this research will provide added benefits by substantiating various assertions and providing new information on the temporal-spatial abundance of larval and juvenile skipjack.

SUMMARY

A set of hypotheses has been generated to account for the origin and movement of exploited skipjack in the eastern and central Pacific Ocean.

The hypotheses postulate that most recruits to the eastern Pacific fishery result from spawning in the equatorial central Pacific. This recruitment stock remains in the fishery for several months, begins to attain sexual maturity, and leaves the eastern Pacific for the equatorial central Pacific where spawning takes place. Some of the evidence upon which the hypotheses are based, and its major features are summarized as follows:

1. It appears that skipjack spawning in the eastern Pacific Ocean is only incidental whereas in the central Pacific spawning is relatively intense. This suggests that the skipjack in the eastern Pacific come from the central Pacific.

2. It was hypothesized from immunogenetic studies and the lack of uniformity in the time-space distribution of skipjack spawning that the skipjack of the central Pacific are not a single homogeneous population unit.

3. The central Pacific was divided into three arbitrarily designated, but likely, zones of origin for skipjack taken in eastern Pacific. These zones are the Hawaiian Zone, the Equatorial Zone, and the Marquesas Zone.

4. It was speculated that skipjack from the Marquesas Zone do not enter the eastern Pacific fishery areas because an unlikely northward component would be required for their migratory path, the Marquesas Zone fish comprise different subpopulations than any of the other areas studied, and a size difference between Tahitian and Hawaiian Zone fish suggests the possibility that fish from the Marquesas Zone may not undergo a relatively high degree of exploitation.

5. A consideration of the relative merits of the Hawaiian and Equatorial Zones as loci for the origin of eastern Pacific exploited fish involved establishing that emigration from the eastern Pacific was spawning-associated. It appears that skipjack samples in the eastern Pacific exhibit relatively high maturity indices for about 9 months each year. This period extends well into the fall suggesting an equatorial destination for the eastern Pacific emigrants.

6. Length-frequency distributions taken from some regions of the eastern Pacific show quarter-to-quarter changes which may be indicative of a more-or-less continual movement of skipjack through the fishery. It appears that this size replacement is of a duration such that it is unlikely that these fish are solely generated in the Hawaiian Islands, thus again suggesting an Equatorial Zone origin for a majority of these fish.

7. There have been three long-distance tag recoveries to date. All three resulted from fish tagged off the Mexican coast. Two were recovered in Hawaiian waters, one in equatorial waters. When compared with the rest of the central Pacific, the Hawaiian region maintains a relatively intense fishery, and therefore the recovery in equatorial waters is more likely to represent a large movement of fish than the two recoveries in Hawaiian waters.

8. It is postulated that as the adolescent skipjack approach the coast of the Americas they are split into a northern and southern contingent; the northern contingent is harvested off the Mexican coast and the southern contingent off Central and South America.

9. Length-frequency distributions from the Hawaiian fishery do not exhibit typical trends such as consistent growth increases; these distributions do, however, show a consistent pattern for adjacent months. Only 3 years of data were available to compare the essentially bimodal Hawaiian length frequencies with the essentially unimodal eastern Pacific length frequencies. For two of the years it appears that skipjack in the small size Hawaiian group have common elements with eastern Pacific size frequencies.

10. The observations of equal numbers of large and small fish in the Hawaiian fishery, a tremendous seasonality in catch, and the existence of at least two subpopulations in Hawaiian waters suggest that there is a component of fish entering the fishery that doesn't originate in the Hawaiian Zone.

11. A prediction of skipjack tuna catch in the Hawaiian Islands has been utilized over the past several years. Large components of variability are not associated with the availability-associated predictive index, and it seems likely that year-class associated phenomena play an important role in controlling the abundance of skipjack in Hawaiian waters.

12. In some years when apparent abundance in Hawaiian waters is high there is a smaller size component of fish in the Hawaiian fishery. This component may be evident as early as February and may in itself serve as a predictive index. An implication is that if year class phenomena can be predicted from the Hawaiian fishery and if the Hawaiian and eastern Pacific fisheries catch skipjack of common origin then it should be possible to predict the abundances of year classes that enter the eastern Pacific fisheries.

13. There is some time interval prior to spawning during which skipjack are unavailable to capture. This has a bearing on sampling problems.

14. The hypothetical nature of this work was emphasized.

15. A critical line for testing the hypotheses in this paper was established among the Hawaiian Islands, the Line Islands, and the Marquesas Islands.

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ADDENDUM

A recent paper received in our Laboratory on June 1, 1965 (Kawasaki, T. 1964. Population structure and dynamics of skipjack in the North Pacific and its adjacent waters. Bull. Tohoku Reg. Fish. Res. Lab. 24:28-47) appears to contain similar conclusions to those in this publication; the present author has not, however, had the opportunity to examine Kawasaki's paper in detail.

B.J.R.

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